

Emergent effects of structural complexity and temperature on predator–prey interactions

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Abstract. Ephemeral aquatic environments are important habitats for a variety of species. They are highly variable with regards to vegetation structure and physico-chemical features that potentially mediate outcomes of biotic interactions. Multiple environmental variables and their emergent impacts on the relationship between prey consumption rate by a predator and prey density (functional response), however, are rarely assessed. Here, we investigated the combined effects of temperature and habitat complexity on the functional response of the freshwater predatory notonectid *Enithares sobria* on the cladoceran prey organism *Daphnia longispina*. A Type II functional response was observed for *E. sobria* predating on *D. longispina* and while temperature and habitat complexity had no effect on the response type, these environmental variables interacted with consequences for the magnitude of the functional responses. Overall, structural complexity favored the predator as greater consumption was observed in the most complex habitat treatment. Temperature effects were also evident although these effects were not unidirectional with regard to treatment factor gradients as predators were the most successful at intermediary temperatures. Furthermore, there was a complex interplay between habitat complexity and temperature, with attack rates being greatest at low and high complexities within intermediate temperatures, while at zero complexity attack rates were greatest at the lowest temperature. The effect of habitat on handling times was only evident in the low temperature treatments which decreased steadily with each increase in complexity. Through the application of functional responses the synergistic effects of multiple environmental drivers on predator–prey interaction outcomes have been highlighted, adding insight into how interactions among species may be affected by natural or artificially induced environmental variability.

Key words: *Daphnia longispina*; early colonizers; *Enithares sobria*; ephemeral ponds; functional response; interaction strength.

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INTRODUCTION

Ephemeral aquatic environments are important habitats for a variety of amphibians, birds, and invertebrates (McCulloch et al. 2003, Ferreira et al. 2012), however, they remain relatively

poorly studied in comparison to permanent freshwater ecosystems (Williams 2006, O'Neill and Thorp 2014). These habitats are naturally variable with regard to depth, vegetation structure and physico-chemical features (Boven and Brendonck 2009, Bird and Day 2014, Bird et al.

2014) and are now often modified by anthropogenic disturbances (Allan et al. 1995, Marty 2005, Hernandez et al. 2006). Organisms that utilize these environments are therefore exposed to a variety of environmental conditions that are likely to affect species interactions. Predation is among the most important of these biotic interactions, playing an essential organizational role in community ecology (Lima 1998, Polis et al. 2000). As predator–prey interactions are influenced by physical factors such as temperature and habitat complexity, their observed outcomes may alter in response to shifting environmental conditions (Vucic-Pestic et al. 2011, Alexander et al. 2012, Brose et al. 2012). This in turn can result in differences in the direction and magnitude of predatory interactions which may influence the stability of prey populations (Abrams 2000). In this regard, this study assessed predator–prey interactions between two key species of ephemeral aquatic habitats in relation to varying habitat complexity and temperature.

Specifically we examined predation by the notonectid *Enithares sobria* toward the cladoceran *Daphnia longispina*. Both cladocerans and notonectids are important components of the invertebrate communities that utilize ephemeral ponds in southern Africa (Allan et al. 1995, McCulloch et al. 2008, Mlambo et al. 2011, Ferreira et al. 2012). These two groups are particularly pertinent as the early colonizing crustacean community is often numerically dominated by cladocerans, and immigrating notonectids are among the first insect predators that these crustaceans encounter (Waterkeyn et al. 2008, Boven and Brendonck 2009, O'Neill and Thorp 2014). As such, during the early stages of an ephemeral pond's hydroperiod, notonectids, and cladocerans are key components in a simple food web.

Habitat complexity and temperature vary considerably in ephemeral aquatic environments and these variables are both likely to alter the strength of *E. sobria*–*D. longispina* interactions. Habitat complexity can modify certain aspects of an organism's performance in its environment, as the physical structure can alter key behaviors, such as, swimming trajectories and ability to hide (Heck and Crowder 1991, James and Heck 1994, Barrios-O'Neill et al. 2014). This may result in reduced predatory efficiency due to the physical structure acting as a barrier to predator

movement (Beekey et al. 2004) or through the provision of refuge space for the prey (Sih et al. 1992, Barrios-O'Neill et al. 2015). Alternatively, predatory species that are more suited for ambush predation incorporating sit-and-wait strategies may perform more efficiently with increased habitat complexity, while certain prey organisms may avoid structure. The effect of increases in habitat complexity on predator–prey interaction strength is therefore determined by predator and prey behavior.

Temperature, on the other hand, has implications for the metabolic demands of an organism (Gillooly et al. 2001, Brown et al. 2004), the effects of which can be expressed through aspects of behavior, with implications for interaction outcomes (Domenici et al. 2007, Englund et al. 2011, Vucic-Pestic et al. 2011). Within the context of predation, the relationship between temperature and interaction strength is complex (Rall et al. 2012). Although metabolic demand must ultimately be subsidized by the acquisition of energy, resulting in correlates between feeding rates and temperature (Domenici et al. 2007, Rall et al. 2012), predation differs from conventional measures of performance in that it is dependent on both the predator and the prey (Ohlund et al. 2014). Performance curves in relation to temperature will likely differ between a predator and prey (Ohlund et al. 2014) making each predator–prey system dissimilar. This variability hampers universal conclusions regarding the scaling of such interactions with warming (Vucic-Pestic et al. 2011). Moreover, while physical variables such as temperature and habitat complexity are key modulators of predation, there remains limited information pertaining to the existence of systematic interactive effects, and potential implications for population dynamics.

To assess predator–prey interactions between notonectids and daphnia we used a functional response approach. The functional response is defined as the relationship between per capita predator consumption and prey density (Holling 1959), and provides insight into how prey populations may be regulated by a predator (Abrams 1990). For example, in a Type II response, an inversely density-dependent relationship results in an increased mortality risk to prey at low densities (Hassell 1978). This may de-stabilize prey populations as high proportions of prey are

consumed when at low densities, driving prey populations to local extinction (Taylor and Collie 2003, Ward et al. 2008). This contrasts sigmoidal Type III responses whereby prey mortality risk decreases at low prey densities (Hassell 1978) and are therefore considered to be more stabilizing, providing prey with a low-density refuge (Hassell 1978, Colton 1987). Often response types can be observed to switch due to the influence of environmental alterations in light (Koski and Johnson 2002), oxygen (Johansson 1999) and, as is the focus here, changes in habitat complexity and temperature (Eggleston 1990, Alexander et al. 2012, Barrios-O'Neill et al. 2015). Understanding mechanisms that mediate changes in functional responses is therefore of importance for understanding how variations in environment can influence population dynamics.

The aim of this study was therefore to use functional responses as a measure of predatory interaction between the early colonizers of ephemeral habitats in the Eastern Cape of South Africa, namely the notonectid *Enithares sobria* and cladoceran *Daphnia longispina*, and determine how this is influenced by temperature and habitat structural complexity. Specifically we aimed to establish whether: (1) *E. sobria* exhibits predatory functional responses toward *D. longispina*, (2) the functional response Type is dependent on structural complexity and/or temperature, and (3) whether one variable can mitigate the effects of the other with regard to the strength of the functional response.

MATERIALS AND METHODS

Sample collection

Enithares sobria and *Daphnia longispina* were collected from a small pond (33°15' S, 26°26' E) in the south-eastern temperate region of South Africa in June 2014. *Enithares sobria*, a common local notonectid, were collected via active searching using a kick net (1000 µm). *Daphnia longispina* were collected using a 57 cm diameter, 200 µm mesh size zooplankton net and were found to be the numerically dominant zooplankton species in the pond, comprising >97% of the catch. In the laboratory, *D. longispina* were isolated from the samples through fraction filtration (1000 µm mesh sieve) followed by individual separation of the species using

pipettes. Populations of *E. sobria* (total length \pm SD: 7.4 ± 0.1 mm) and *D. longispina* (1.9 ± 0.2 mm) were sorted into separate aquaria ($46 \times 23 \times 31$ cm) filled with filtered (strained through 20 µm mesh sieve) water from the collection site. Both predators and prey were then exposed to three contrasting acclimation temperatures of $14 \pm 0.5^\circ$, $22 \pm 0.5^\circ$ and $30 \pm 0.5^\circ\text{C}$, each with a 12:12 h light:dark photoperiod cycle in temperature controlled environmental rooms. Both predator and prey species were acclimated at these temperatures for a period of 7 d prior to experimentation. *Daphnia longispina* were fed ad libitum on an algal culture of *Cryptomonas curvata* for the duration of the acclimation period and in the same way *E. sobria* were fed on *D. longispina* for the first 5 d of acclimation and starved for the last 48 h.

Experimental design

To quantify the *E. sobria* functional response toward *D. longispina* we used a full factorial design with three test temperatures and three levels of habitat complexity, resulting in nine treatment regimes. Experiments were carried out in aerated circular polyethylene containers (66 mm diameter) filled with 250 mL filtered water from the collection site. The experimental habitat structural complexity was simulated using stalks of *Cyperus eragrostis* (10 cm long, 0.4 cm diameter). Containers were placed in temperature regulated water baths at either $14 \pm 0.1^\circ$, $22 \pm 0.1^\circ$, or $30 \pm 0.1^\circ\text{C}$, corresponding with the respective acclimation temperatures. The *C. eragrostis* stalks employed were collected from the same ponds as the experimental animals and washed to remove any attached epiphyton. Complexity within each container was established as high (four stalks), low (two stalks) or zero (no stalks) (Fig. 1) which represented the range of small scale habitat complexity found in the ephemeral ponds (R. Wasserman, personal observation).

For each of the nine treatments, individual *E. sobria* were presented with *D. longispina* at seven prey densities (5, 10, 20, 30, 60, 90, and 140 individuals, $n = 4$ per prey density). In all cases containers were stocked with the *D. longispina* prey 6 h prior to the introduction of the predatory *E. sobria*. Once stocked, predators fed undisturbed

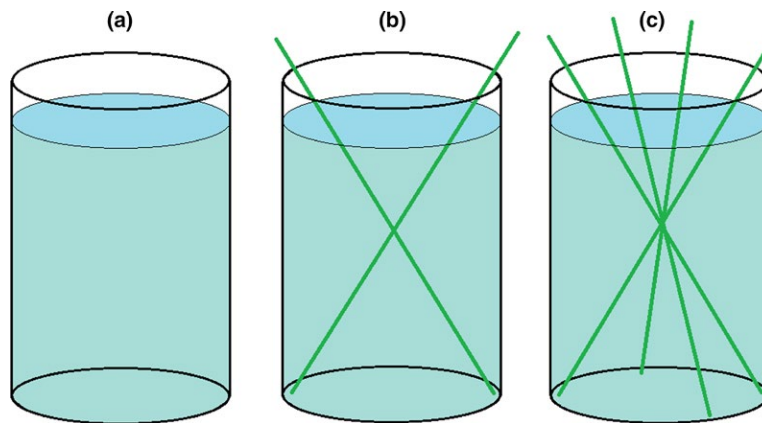


Fig. 1. Illustration of habitat complexity treatments showing (a) zero, (b) low, and (c) high complexity.

for 18 h after which they were carefully removed from the containers, along with the *C. eragrostis* substrate. All remaining prey were collected in a 60 μm mesh sieve and counted under a dissecting microscope at 12 \times magnification. Controls at the same prey densities containing no predators were run simultaneously, with the *D. longispina* collected and counted as described above after 18 h.

Data analysis

Differences in overall prey consumption among habitat complexities, temperature and prey densities were assessed using a generalized linear model (GLM) with a Poisson error distribution. As there was no interaction found between habitat complexity and prey density or between habitat complexity, temperature and prey density, these interaction terms were removed to identify the minimum adequate model (Crawley 2007). Significant effects in the model were analyzed with Tukey's contrast *post hoc* tests, performed using the package "Multcomp 1.2-8" (Hothorn et al. 2008).

The Type of functional response was first determined using logistic regression that tests for a negative linear coefficient (fitted using maximum likelihood) in the relationship between the proportion of prey eaten and prey density. This would indicate a Type II functional response (Juliano 2001). We then modeled by maximum likelihood estimation (Bolker 2008) Type II functional responses (see Results) using the "Random Predator Equation" (Rogers 1972), which is ap-

propriate where prey are not replaced as they are consumed, such was the case here (Juliano 2001);

$$N_e = N_0 \{1 - \exp[a(N_e h - T)]\}$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack constant, h is the handling time and T is the experimental period.

So as to compare the obtained functional responses, data sets were non-parametrically bootstrapped ($n = 2000$) to construct 95% confidence intervals around functional response curves and their associated parameters. The random predator equation was fitted to each bootstrapped data set using starting values of a and h that were obtained from the original maximum likelihood estimates. As bootstrapping allows data to be considered in terms of populations, if the confidence intervals do not overlap we are able to deduce that the functional responses and/or their associated parameters are different. All analyses were carried out in R v. 2.15.1 (R Development Core Team 2012) and functional response modelling was undertaken using the "frair" package (Pritchard 2014).

RESULTS

Control *D. longispina* had high survival in all replicates (>98%), thus experimental deaths were attributed to consumption by *E. sobria*, which was also directly observed. Habitat complexity influenced the overall numbers of *D. longispina* consumed by *E. sobria* ($F_{2,36} = 54.32$,

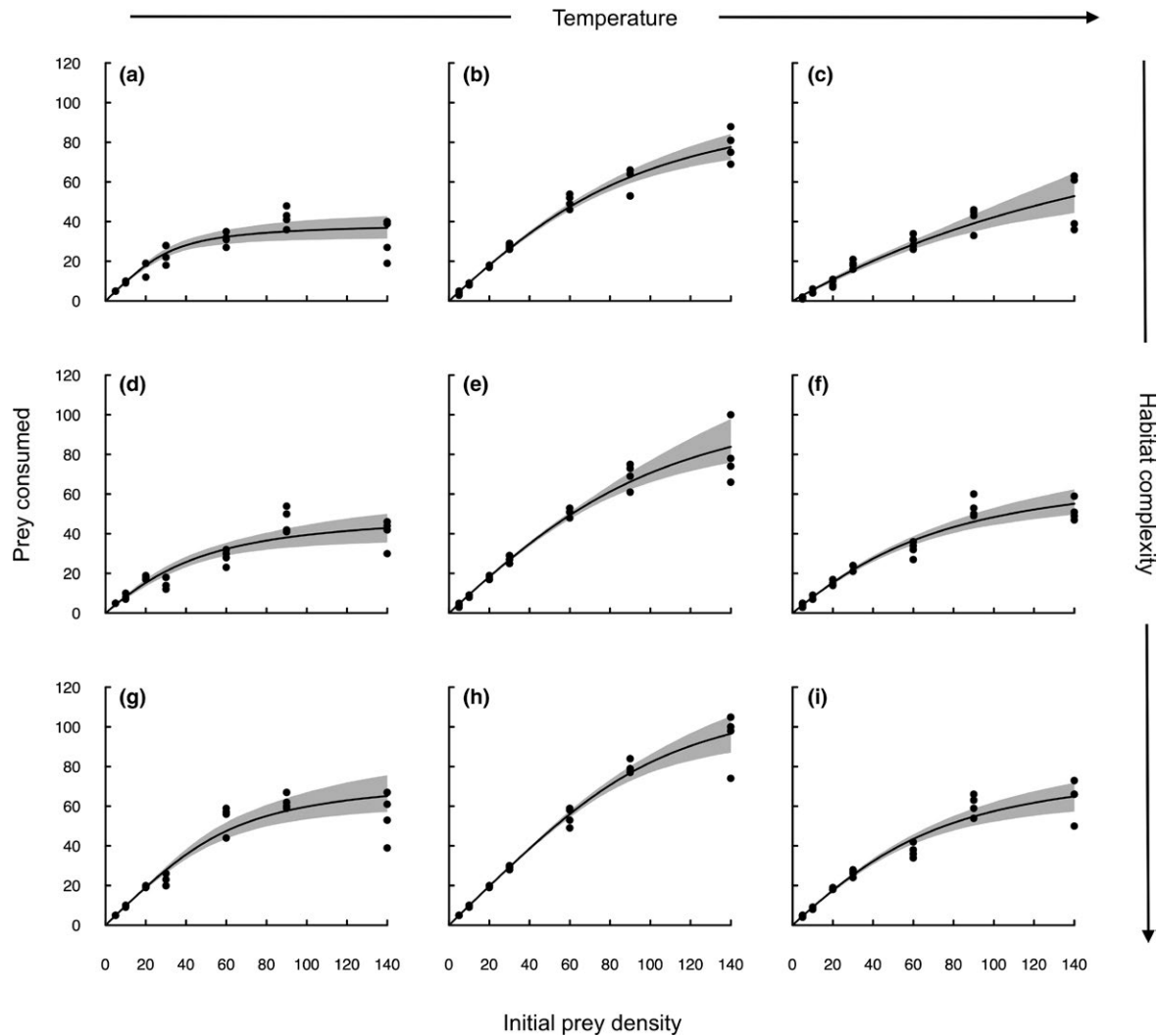


Fig. 2. Type II functional responses of *Enithares sobria* towards *Daphnia longispina* at 14 (a, d, g), 22 (b, e, h), and 30°C (c, f, i) at zero (a, b, c), low (d, e, f), and high (g, h, i) habitat complexities. Shaded areas are 95% confidence intervals. Raw data points are overlaid.

$P < 0.001$), with greater consumption in high habitat complexity compared to both low (Tukey's test, $P < 0.001$) and zero (Tukey's test, $P < 0.001$) complexities. There was no difference in number of prey consumed between zero and low habitat complexity (Tukey's test, NS). There was a significant effect of temperature ($F_{2,36} = 115.54$, $P < 0.001$), and this was driven by greater consumption at 22°C compared to both the 14° and 30°C treatments (Tukey's test, $P < 0.001$). There was also greater prey consumption in higher density treatments ($F_{6,36} = 666.50$, $P < 0.001$). A significant interaction

was detected between "habitat × temperature" ($F_{4,36} = 4.58$, $P < 0.01$) owing to increased consumption in high complexity treatments at each temperature in comparison to those in reduced habitat treatments (Tukey's tests, $P < 0.001$). A significant interaction was also found between "temperature × prey density" ($F_{12,36} = 6.46$, $P < 0.001$).

In each habitat type and temperature combination, *E. sobria* exhibited Type II functional responses towards *D. longispina* (Fig. 2; Table 1). We have presented these results with respect to habitat complexity owing to the clear

Table 1. Parameter estimates from logistic regression analyses of proportion of prey killed against initial prey density in high, low and zero habitat complexities at 14°, 22°, and 30°C.

Habitat complexity	Temperature (°C)	Intercept value	N_0 value	FR type
High	14	3.1992**	-0.0259**	II
	22	4.1356**	-0.0243**	II
	30	1.9872**	-0.0156**	II
Low	14	1.1886**	-0.0148**	II
	22	2.6202**	-0.0165**	II
	30	1.3339**	-0.0131**	II
Zero	14	1.9174**	-0.0231**	II
	22	2.2987**	-0.0151**	II
	30	0.2686*	-0.0057**	II

Note: Values for the intercept and first-order (N_0) terms are presented with significance levels; * $P < 0.01$, ** $P < 0.001$.

differences that occur across temperatures in each of the habitat treatments (Fig. 2). Overall, *E. sobria* had greatest functional responses in the 22°C treatments at each habitat complexity. There were, however, subtle differences between the responses across the range of densities tested. At zero complexity, predation was similar and heightened at low *D. longispina* densities in the 14° and 22°C treatments in comparison to the warmer 30°C trials (Fig. 2a–c). However, this pattern broke down and the 14° and 22°C treatment responses diverged considerably as prey density increased. At intermediate densities of prey, predation by *E. sobria* increased and was greater than that at the lowest temperature. In low habitat complexity treatments, the functional response of *E. sobria* at 22°C was heightened in comparison to the other temperatures across the range of prey densities (Fig. 2d–f). In high habitat complexity treatments we found similar results as in low complexities, however, the divergence of predation at intermediate temperatures did not occur until prey density was greater than in the previous treatment, as indicated by the convergence of the 95% confidence intervals at low prey densities (Fig. 2g–i).

Bootstrapped parameter estimates of attack rates and handling times provided information on the subtle differences between the functional responses. Attack rates were generally found to be significantly greater at 22°C in comparison to 30°C in all habitat types (Fig. 3a–c) as evidenced

by a lack of overlap in the 95% confidence intervals. There was, however, no such difference between 14° and 22°C treatments. Attack rates at 14°C were not found to differ across habitat treatments according to confidence intervals. Those at 22°C were heightened in high habitat complexities (Fig. 3c) whilst those at 30°C were reduced in zero habitat treatments (Fig. 3a). Handling times were found to be quite consistent across the habitat treatments at 22° and 30°C (Fig. 3d–f). Those from 14°C treatments, however, were more susceptible to change and were found to decrease from zero habitat (Fig. 3d) to high habitat complexity (Fig. 3f). At zero and low habitat complexity, handling times were significantly greater at 14°C compared to 22° and 30°C (Fig. 3d, e). However, this parameter was comparable across the three temperatures at high habitat complexity (Fig. 3f).

DISCUSSION

This study shows that environmental variables significantly alter interactions between pioneer predators from ephemeral ponds and their main prey. Temporary wetlands such as ephemeral ponds are generally more variable habitats than permanent water bodies with regard to their physical, chemical, and biotopic characteristics, largely due to the intrinsic dynamic nature of these environments (Batzer et al. 2004, Williams 2006, Waterkeyn et al. 2008). In such habitats, however, quantitative studies assessing the role of environmental factors in structuring biotic assemblages are scant, resulting in a relatively poor understanding of the ecology of ephemeral aquatic habitats (Batzer et al. 2004). The results presented here demonstrate that temperature and habitat complexity alter predator–prey dynamics between *E. sobria* and *D. longispina*, but also that these physical factors interact in complex ways which may confound expectations based on broad generalizations.

We observed the notonectid *E. sobria* to exhibit predatory functional responses towards *D. longispina* across a range of habitat and temperature combinations. The form of functional response was not, however, dependant on either habitat or temperature manipulation, with Type II responses observed throughout. This is in contrast to a number of other studies that demonstrate

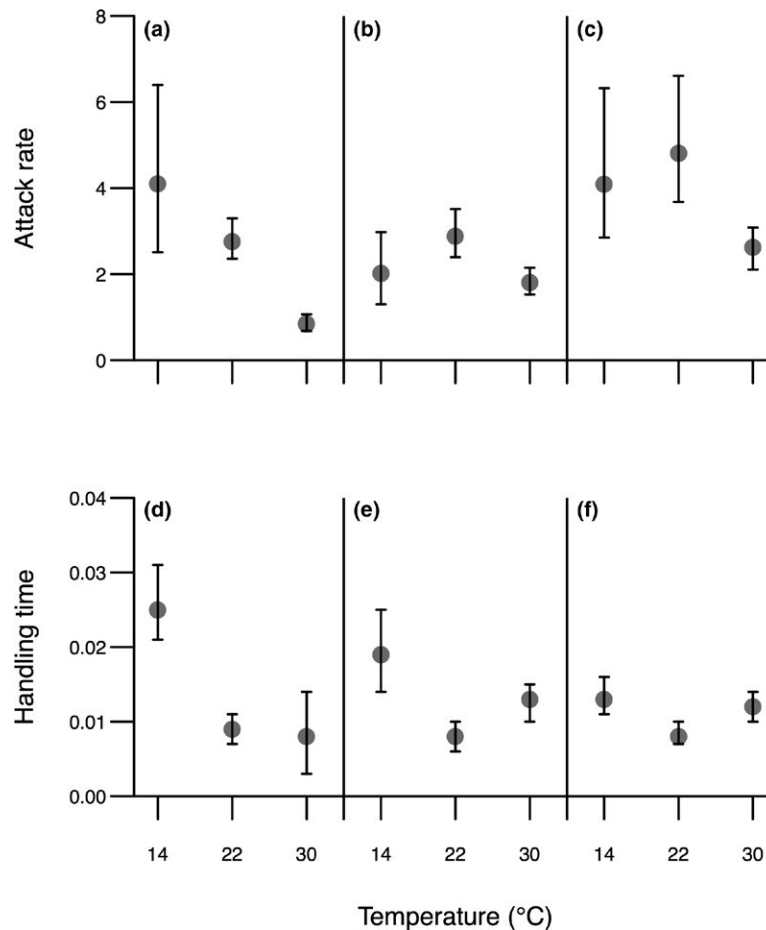


Fig. 3. Parameter estimates for attack rates (a) and handling times (h) for *Enithares sobria* predating on *Daphnia longispina* in zero (a, d), low (b, e), and high (c, f) habitat complexities at 14°, 22°, and 30°C. Points are original MLE values and error bars are bootstrapped 95% confidence intervals.

switching in response from Type II to III with environmental changes, such as with the addition of habitat complexity (Alexander et al. 2012) or alterations in light intensity (Koski and Johnson 2002). This could have implications for the long-term persistence of the daphniid prey in these systems, as Type II functional responses de-stabilize prey populations, as a result of high proportional consumption of prey at low densities (Taylor and Collie 2003, Ward et al. 2008). Indeed, cladocerans are often the first zooplankters to be eliminated when predators arrive (Pajunen and Pajunen 2003, Feniova et al. 2015). Thus, the long-term persistence of these cladocerans at the landscape scale may depend acutely on metapopulation dynamics, rather than the form and magnitude of proximal interactions per se (Huffaker 1958).

When assessing the treatment (habitat complexity and temperature) factors separately, we observed that each had implications for predation. Overall, structural complexity favored the predator as greater consumption was observed in the most complex habitat treatment. This suggests that structure is an important aspect influencing the success of predation by *E. sobria*. The effect of temperature on the strength of the functional response between *E. sobria* and *D. longispina* was also evident. Unlike structural complexity, these effects were not unidirectional with regard to treatment factor gradients, signifying peak performance by the predator at some temperature optima, consistent with the environmental matching hypothesis (Iacarella et al. 2015). Overall, a greater consumption of *D. longispina* was

observed at intermediate temperatures (22°C), suggesting that both low and high temperature extremes can influence the dynamics of this predatory interaction. Such effects of temperature may be a result of physiological constraints of either the predator, prey or a combination of both. The greater significance of this is that interactions within ephemeral ponds are in a state of flux owing to the highly dynamic nature of such systems and the frequent and extreme changes in environmental conditions that typically define these habitats (McCulloch et al. 2008, Boven and Brendonck 2009, Bird and Day 2014, Brendonck et al. 2014, O'Neill and Thorp 2014).

When assessing the emergent impacts of both temperature and habitat complexity, however, we observe that one factor can, under certain conditions mitigate the effects of the other. For example, differences among attack rates across temperatures are altered depending on the level of habitat complexity, with low and high complexities resulting in the greatest attack rates at intermediate temperatures, while at zero complexity attack rates are greatest at the lowest temperature. Alternatively, under certain circumstances one factor can have little influence over the other, such as the attack parameter at the lowest temperature, which differed little across habitats indicating that changes to structural complexity at this temperature have limited implications for the attack rates of the predators. Differences were, however, observed in the remaining temperature treatments with increases in habitat complexity resulting in heightened attack rates, likely an aspect of increased encounter rates between predator and prey.

Across complexity treatments, handling times were longer at the lowest temperatures. Handling time is a measure of both the actual physical handling of the captured prey by the predator as well as the digestion time (Jeschke et al. 2002). Jeschke et al. (2002) have shown that most predators are digestion limited, with this aspect of handling time often increasing with decreasing temperature. However, notonectids capture prey using raptorial legs and consume them using a rostrum, whereby digestive juices are injected into captured prey with the digested material then sucked from the victims (Sanchez et al. 2008). Therefore, unlike a predator that consumes prey in its entirety, the digestion time of

notonectids is closely coupled with the physical handling time. As a result, increases in encounter rates may have resulted in increases in partial consumption and therefore shorter handling time, as was also observed in preliminary trials assessing notonectids attack and prey handling (*unpublished data*). We therefore suggest that in this study the longer handling times at low temperature treatments could have been an aspect of slower swimming speeds and consequent lowered predator-prey encounter rates, as well as increased required digestion times by the predators at these temperatures.

The shortest handling times were found at the intermediate temperatures, consistent with the temperature—feeding rate scaling predictions of Rall et al. (2012). Habitat complexity, however, seemed to mitigate the effects of temperature on handling times. Within each habitat complexity regime, differences among handling times (in relation to temperature) decreased with an increase in complexity as handling times at the high complexities were the most similar across temperatures. It is therefore highly likely that increases in habitat complexity facilitate greater encounter rates between predators and prey and, therefore, shorter handling times through increased partial consumption. In addition to the reduction in handling time, habitat complexity increased attack rate at intermediate and high temperatures. The increased structure therefore likely facilitated attack-launch habitat, augmenting vertical use of the environment by *E. sobria*. Notonectids often attack prey from perch sites at the water surface or submerged structures (Gergs and Ratte 2009). This suggests that structural changes in the physical environment (habitat complexity) and its effects on attack rate and handling time, may override some of the effects of temperature in this regard, which are ultimately linked to the physiology of the predator and the prey.

Temperature is an important factor regulating performance in all animals (Ward and Stanford 1982), therefore differences in thermal optima between a predator and its prey will likely affect predator-prey interaction outcomes (Englund et al. 2011). Maximum swimming speed, escape/attack response time and behavior of both predator and prey can all be dependent on temperature (Gerritsen 1982, Ziarek et al. 2011, Rall et al. 2012). It is likely that the changes in temperature are re-

sulting in differential predation rates that, under certain habitat conditions, are no longer mediated owing to the absence of structure. The interplay of these two factors therefore has important repercussions for predator–prey interaction outcomes. In addition, habitat can result in reduced predatory efficiency which can be attributed in part to increases in search times (Heck and Crowder 1991), often as a result of the physical structure acting as a barrier to predator movement (Beekey et al. 2004) but also the provision of refuge space for the prey species (Sih et al. 1992, Barrios-O'Neill et al. 2015). However, as reported here, species that are more suited for ambush predation incorporating sit-and-wait strategies may perform more efficiently since encounter rates depend explicitly on prey movement. Indeed some ambush predators are not affected by complexity at all (James and Heck 1994), and, as in the case of *E. sobria*, can even show an increase in capture success (Flynn and Ritz 1999). As such, each predator–prey system is unique (Jeschke et al. 2002) and variability in thermal comfort and optima between a given predator and its prey could potentially shift interaction outcomes, depending on the temperature. It seems that such differences can, however, be mediated by other environmental factors such as habitat complexity, as was the case with attack rates and handling times in this study. Since the mechanisms by which temperature and habitat complexities alter attack rates or handling times differ, these effects may under certain circumstances counter one another when acting in combination.

While pairwise interactions such as those simulated in this study do not necessarily translate to community-level dynamics, functional responses are a fundamental component of food web ecology (Jeschke et al. 2002, Barrios-O'Neill et al. 2015). The importance of species-specific interactions should, therefore, not be overlooked (Rall et al. 2011), particularly those interactions between key components of food-webs. Since both predator and prey are unlikely to respond to environmental changes such as temperature, depth or light availability in precisely the same way, environmental alterations are expected to shift the balance in favor of one or the other. These and other real world components are important considerations in predator–prey dynamics (Barrios-O'Neill et al. 2014). The findings here clearly highlight a complex interplay between the two environmental

variables of habitat and temperature. These are important to consider in the context of habitat degradation where the interaction of such drivers may result in synergistic effects that may not be predicted from single drivers on their own. Here we have shown, through the application of functional responses, that temperature, habitat complexity and their interaction are important determinants of predator–prey dynamics which may have implications for the stability and functioning of an ecological system.

Studies such as the present, that assess combined effects of multiple physical factors on biological interactions have relevance for communities in pristine environments, but can also add insight into how interactions among species are affected by environmental disturbances.

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